Complex plant traits

Jansen, Ritsert C.

Published in:
Trends in Plant Science

DOI:
10.1016/S1360-1385(96)80040-9

Publication date:
1996

27 Dudits, D., Bögre, L. and Györgyey, J. (1991) Molecular and cellular approaches to the analysis of plant embryo development from somatic cells *in vitro*, *J. Cell Sci.* 99, 473–482
28 Kalloo, G. and Chowdhury, J.B., eds (1992) *Distant Hybridization of Crop Plants* (Monographs on Theoretical and Applied Genetics 16), Springer
29 Zenkteler, M. (1995) Self and cross pollination of ovules in test tubes, in *Current Issues in Plant Molecular and Cellular Biology* (Terzi, M., Cella, R. and Falavigna, A., eds), pp. 191–199, Kluwer
30 Jürgens, G. (1995) Axis formation in plant embryogenesis: Cues and clues, *Cell* 81, 467–470
31 Sheridan, W.F. and Clark, J.K. (1993) Mutational analysis of morphogenesis of the maize embryo, *Plant J.* 3, 347–358
32 Dresselhaus, T., Lörz, H. and Kranz, E. (1994) Representative cDNA libraries from few plant cells, *Plant J.* 5, 605–610
33 Foltz, K.R., Partin, J.S. and Lennarz, W.J. (1993) Sea urchin egg receptor for sperm: Sequence similarity of binding domain and hsp70, *Science* 259, 1421–1425
34 Campenot, M.K. *et al.* (1992) Zea mays embryo sacs in culture. I. Plant regeneration from 1 day after pollination embryos, *Am. J. Bot.* 79, 1368–1373
35 Mól, R., Matthys-Rochon, E. and Dumas, C. (1993) *In-vitro* culture of fertilized embryo sacs of maize: zygotes and two-celled proembryos can develop into plants, *Planta* 189, 213–217
36 Karrer, E.E. *et al.* (1995) *In situ* isolation of mRNA from individual plant cells: Creation of cell-specific cDNA libraries, *Proc. Natl Acad. Sci. USA* 92, 3814–3818
37 Richert, J. *et al.* (1996) A reverse transcriptase–polymerase chain reaction assay for gene expression studies at the single cell level, *Plant Sci.* 114, 93–99

Erhard Kranz and Thomas Dresselhaus are at the Centre for Applied Plant Molecular Biology, AMP II, University of Hamburg, Ohnhorststr. 18, D-22609 Hamburg, Germany.

Complex plant traits: time for polygenic analysis

Ritsert C. Jansen

Currently, mapping of genes for complex traits is an area of active theoretical research at the interface of genetics and statistics. Much progress has been made over the past few years in handling statistically complex but realistic multilocus models. Here, I describe the state of the art and discuss new opportunities for the genetic dissection, understanding and manipulation of complex biological processes.

For many plant processes, we know nothing about how many genes are involved, where the genes are located on the chromosomes, what effects the genes have and how the genes interact. The unknown loci of the genes on the chromosomes are commonly referred to as 'quantitative trait loci' (QTLs). Fundamental plant biology and plant breeding would be revolutionized if techniques for dissecting multilocus systems were available and could be applied routinely. Important progress has been made at the molecular level by the development of molecular markers[1,2]. Developments in the past few years indicate that further progress can also be expected at the statistical level. Currently, methods based on single-QTL models are widely used, but they are intrinsically inappropriate for multilocus systems. It is likely that new methods based on multilocus models will provide the method of choice for the future. Here I describe the main features of these models and discuss their prospects and limitations*. Two examples are provided of how the methods have been used recently in fundamental research on plant development and in breeding for disease resistance.

Mapping quantitative trait genes

If a quantitative trait is encoded by many genes, the distribution of trait values may appear continuous because numerous genotypes exist in the population. If the trait is affected by a few genes, it may still show continuous variation when environmental factors influence the trait. In most situations, genetic and environmental factors are active and genetic dissection is virtually impossible from the trait data alone. Molecular markers provide plant scientists with new and advanced technology for genetic analysis[1,2]. The crucial idea is that observed marker genotypes can be used to obtain indirect information on the genotype at a target gene (Fig. 1). This only works well if the target gene is located close to a marker, so that alleles of the marker and target gene are linked. Therefore, ideally the set of markers should cover all chromosomes. Genetic marker maps are now available for many plant species[3].

Conventional QTL mapping: methods for one QTL

The traditional approach to the mapping of QTLs is to consider markers individually[4] (Fig. 1). For each genotype (allelic constitution) of a marker, the genotypic mean can be calculated as the mean of the trait values of the plants with that genotype. If the marker is tightly linked to the target gene, marker and QTL alleles will be associated and as a consequence the genotypic means of the marker will be different. This can be tested statistically and the likelihood for the presence of a putative QTL can be plotted at the marker positions along the chromosomes, so as to present the evidence for QTLs at the various positions in the genome.

Methods have also been developed that can assess the QTL likelihood at all locations, that is, also in intervals between markers. Currently, the 'interval mapping' method[5] is widely used [and the computer program MAPMAKER/QTL (Ref. 6) is treated as an 'industry standard']. As in the traditional approach, we would like to calculate genotypic

*In addition, see the December 1995 Special Issue of *Trends in Genetics* on multifactorial inheritance.

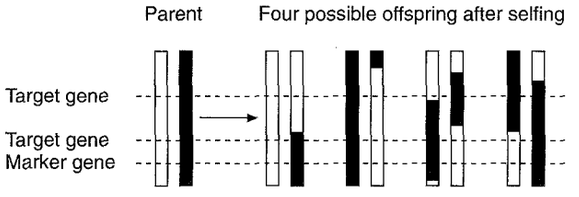

Fig. 1. Example of how marker information can be used to obtain information on the genotype of a target gene in a segregating population. The genotype of the marker gene (white or black for each gamete) can be observed, but not that of the target gene. If the marker is near (tightly linked) to the target gene, most gametes will not be recombinant for the two loci: white is associated with white, and black is associated with black (see lower target gene and marker gene). Therefore, in the progeny an indirect observation of the genotype at the target gene can be obtained from marker information. If the distance is larger, the occurrence of recombination must be taken into account; for instance, if the observed marker genotype is black/white, the unobserved genotype at the target gene may be white/white, black/white, white/black, or black/black (see upper target gene and marker gene). The classes white/black and black/white may be pooled if reciprocal effects on the trait are ignored.

means at a target locus in the interval, but this is impossible because the genotypes are not observed. In interval mapping, however, probabilities are assigned to the possible genotypes of the target locus – these probabilities depend on the genotypes of flanking markers and on the trait values (step 1). For each genotype of the target locus, the genotypic mean can be calculated as the weighted average of all trait values, where the weights involved are the probabilities assigned to that genotype (step 2). Again, significant differences between genotypic means indicate the presence of a QTL. Unfortunately, weights depend on unknown trait parameters and cannot be calculated directly. The key to this problem is to set the parameters to initial values and to iterate the two steps until subsequent updates of weights and parameters show no more changes[7].

It should be noted that some authors employ the 'LOD-score' ('logarithm of odds score') for QTL likelihood, whereas I and others use 'the likelihood ratio test'; the latter is $2\log_e(10)$ times the former.

Recent advances in QTL mapping: methods for two or more QTLs

Lander and Botstein[5] made the first move towards fitting two QTLs simultaneously. Generalization to more QTLs was hampered by the complexity of the statistical models describing multilocus systems. Exact methods[7] and approximate methods[8–10] have been developed for dissecting the effects of two or three linked QTLs. For multilocus models two methods have been developed recently, the genetic concepts of which are more or less identical, namely MQM (multiple-QTL model or marker-QTL-marker) mapping[11,12] and composite interval mapping[13,14].

By extending the interval mapping algorithm, a model with any number of QTLs can be fitted to data. However, exact computations are not feasible because of the extremely large number of possible genotypes at the QTLs (e.g. 3^{10} per plant for ten QTLs in the F_2 generation). A way to overcome this problem is obtained by noting that for precision mapping of a QTL in a particular interval the positions of other QTLs need not be assessed as accurately[7]. The basis of MQM mapping and composite interval mapping consists of the precision mapping of a single QTL in a certain interval (like in interval mapping), while other QTLs are 'placed' at associated marker positions. Since the positions of the QTLs are generally unknown, the question is which markers should be used. This issue will be discussed in detail later (see *Detection of markers near QTLs*). Here it suffices to say that in MQM mapping only markers in an initial set of plausible QTL regions are used, whereas in composite interval mapping all markers of all chromosomes are used; in both methods, markers near the interval under study are excluded. It should be noted that preselection of markers is also possible in composite interval mapping (see below)[14].

The two steps of the algorithm of composite interval mapping and MQM mapping now consist of updating the weights (genotype probabilities) by using the current estimates of trait parameters, and updating the estimates of trait parameters by using the current weights[11,14].

QTLs are said to be present in those regions where the QTL likelihood is larger than a specified threshold. But what value of the threshold corresponds to what significance level? The problem of choosing appropriate thresholds has been dealt with in various ways within the framework of interval mapping[5,15–18]. For composite interval mapping, simulation work has lead to formulae for the threshold as a function of a genome-related significance level[12,14]. For MQM mapping, simulation studies have demonstrated that the thresholds derived for conventional interval mapping are still valid in many situations[12].

Further extensions: incomplete marker information and multiple traits

In practice, marker genotypes are sometimes ambiguous or unknown (often about 5% of the observations on markers). One way to overcome the problem is obtained by noting that any missing genetic data, for QTL as well as for marker loci, can be recovered by considering the possible genotypes and calculating weights associated with them[11]. In addition to data missing by chance, other types of marker data may be missing naturally, for instance when markers are dominant and the heterozygote cannot be distinguished from one of the homozygotes. For large progenies with very incomplete marker information, exact computations are not feasible because of the extremely large number of possible genotypes at marker and QTL loci. Very recently, the original MQM mapping method has been extended to cope with such complex situations[19]. A small sample of possible genotypes rather than the set of all possible genotypes is now considered. However, the same iteration scheme is retained. The problem of incomplete marker information is illustrated in the second application (see later).

In many QTL experiments, more than one trait is scored for the same plants. Recently, the univariate approach of composite interval mapping has been extended to a multivariate approach in which a joint analysis of multiple traits is possible[20]. This approach provides a formal method for quantifying pleiotropy or testing pleiotropy at a single QTL versus linkage of two or more QTLs. The method can also be used to analyse experiments in which one trait is measured in more environments (equivalent to multiple traits). Interaction between the environment and QTL can now be part of the model. The interaction of the environment and

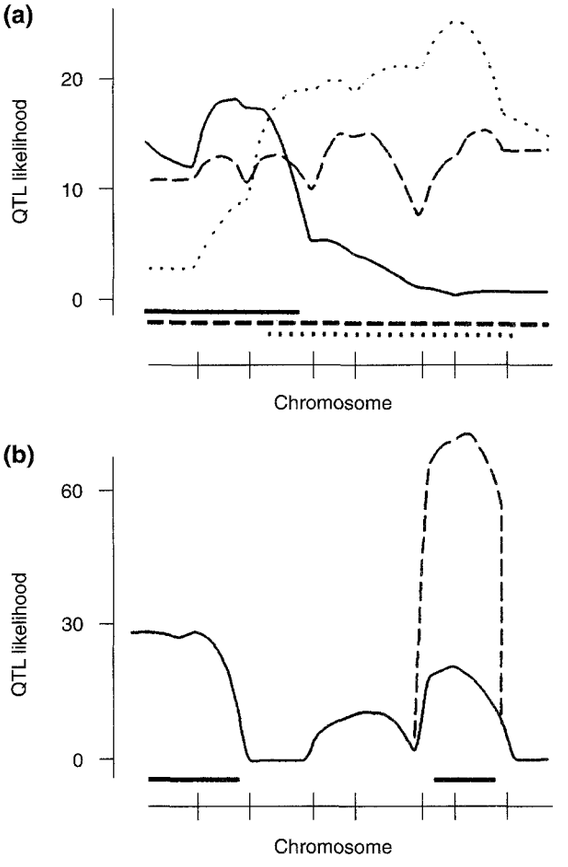

Fig. 2. Quantitative trait locus (QTL) mapping for flowering time in *Arabidopsis* under several different environmental conditions. In interval mapping, data can only be analysed for each environmental condition separately. In contrast, with MQM (multiple-QTL model or marker-QTL-marker) mapping a joint analysis is possible and multiple QTLs with QTL–environment interactions are now part of the model.

QTL likelihood curves and QTL regions for chromosome 2 (52 centimorgans) are shown. In each of the two plots the horizontal axis represents the chromosome, and the tick marks across the horizontal axis indicate marker positions. Bars above the horizontal axis indicate 95% confidence intervals (QTL regions) for the QTLs detected.

With interval mapping (a) there is evidence for QTL activity, but QTL likelihood curves are rather flat over a large chromosome region and, as a result, QTL regions are large. In the interval mapping plot, QTL likelihood curves and QTL regions for three out of the six environments are shown. Patterns of curves and bars correspond: dashed curve, short days; solid curve, long days; and dotted curve, continuous light. QTLs are detected in regions where the QTL likelihood is larger than 10 (the threshold at a 5% genome-related significance level).

With MQM mapping (b) two QTLs with effects of equal sign are detected on chromosome 2 and one of them displays QTL–environment interaction (QTL × E). In the MQM mapping plot the solid curve represents the QTL likelihood for a QTL without QTL × E; the dashed curve represents the QTL likelihood for a QTL with QTL × E [plotted only in the region where QTL × E was detected; in this region the QTL has a large effect in continuous light, a moderate effect in short days and no effect in long days (data not shown)]. The threshold is 11 for QTL detection and 22 for QTL × E detection (at a 5% genome-related significance level).

QTL can also be fitted in the framework of MQM mapping[21]. For these complicated situations, the thresholds used for QTL detection can be assessed by various computer-intensive methods[18,21].

Although the models that are used in MQM mapping and composite interval mapping assume the absence of interaction between QTLs (epistasis), such interactions can be modelled easily. Unfortunately, the number of parameters relative to the amount of data increases rapidly. Finally, models for disease severity scores or quality data can also be used in the framework[22].

High resolution mapping

Often the ultimate goal of QTL mapping experiments is to set the stage for applied or fundamental use of QTLs, for instance in marker-assisted breeding[1] or map-based cloning[23]. High power and precision QTL mapping will certainly contribute to more successful QTL use. Here I review the progress made in the development of multilocus methods.

Improved power and precision

Many traits of biological and agricultural interest are of a polygenic nature. Experimental results have shown, however, that in many instances 30–80% of the trait variation can be explained by a few QTLs with major effects[2]. In many experiments, individual QTLs even account for 10–50% of the trait variation[2]. In general, the power for the detection of a QTL depends on the ratio between the trait variance induced by the QTL and the residual variance, which consists of environmental and unexplained genetic variation. In single-QTL methods, QTLs are mapped individually, ignoring the effects of other QTLs (which may or may not be mapped). In contrast, multiple-QTL methods eliminate the genetic variance caused by other QTLs and consequently reduce the residual variance.

Now assume, for example, that a single QTL explains 5% of the trait variance in a tomato F_2 experiment of 200 plants, and assume that other unlinked QTLs explain another 55% of the trait variance (i.e. the residual variance is 40% of the trait variance). The probability of detecting a 5% QTL by interval mapping is about 0.29 (Ref. 15). If we eliminate the effects of other QTLs by using a multiple-QTL approach, the ratio of the variance induced by the 5% QTL and the residual variance is 5 : 40 (which is approximately 11 : 89). This is now equivalent to the detection of a single QTL explaining 11% of the trait variance, and the probability of detection is about 0.79 (Ref. 15). Simulation work indicates that this maximum gain of power can be obtained by MQM mapping[12].

Power increases if more plants are tested or if genotypes are replicated (e.g. by cloning). This increase may be much larger for multiple-QTL methods than for single-QTL methods. If genotypes are replicated, this will decrease the environmental part of the trait variation. With four replicates the ratio between the variance induced by the 5% QTL and the residual variance is 5 : (55 + 40/4) (which is approximately 7 : 93) for a single-QTL approach, and thus the situation

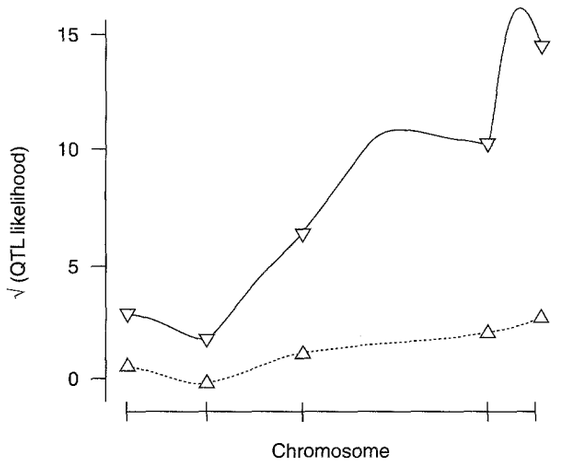

Fig. 3. Quantitative trait locus (QTL) mapping for *Fusarium* resistance in lily (*Liliaceae*) with dominant markers in an outbred progeny. Here, at each locus three different alleles may be present in the progeny[19]. A dominant marker detects only the presence or absence of one specific allele at the marker locus. In the traditional approach markers are analysed individually and only the difference between the plants with 'marker band present' and the plants with 'marker band absent' can be tested at each marker locus. In contrast, with MQM (multiple-QTL model or marker-QTL-marker) mapping the effects of the three possible alleles can be unraveled. Multiple QTLs and multiple alleles at each locus are now part of the model. QTL likelihood curves for chromosome segment 2 (117 centimorgans) are shown. The horizontal axis represents the chromosome, and the tick marks across the horizontal axis indicate marker positions. In the markers-one-by-one approach (dotted line) QTL likelihood is assessed at marker positions only. In MQM mapping (solid curve) QTL likelihood is assessed at marker positions and halfway between markers only, because of the computational effort involved. The thresholds for QTL detection at a 5% genome-related significance level are 3.5 and 4.5, respectively.

is now equivalent to that of a 7% QTL. But the ratio becomes 5:(40/4) (which is approximately 33:66) when using a multiple-QTL method, equivalent to a 33% QTL; the probability of detecting such a QTL is equal to 1.00 for MQM mapping[12].

In the case of linked QTLs, the comparison of the single-QTL and multiple-QTL approaches leads to even more dramatic differences. In interval mapping, linked QTLs with opposite effects may go unnoticed because of their mutual neutralization[12,14]. Furthermore, in interval mapping, linked QTLs with effects in the same direction tend to be mapped as a single QTL at some intermediate position on the map[10,12]. This may even happen for QTLs that have major effects and are far apart. For example, assume that two QTLs are 40 centimorgans (cM) apart and explain 50% of the trait variance in a backcross population of 100 individuals with a 1000 cM genome. If the two QTLs have opposite effects, the probability of detection is 0.42 for each QTL by interval mapping and 0.97 by MQM mapping[12]. If the two QTLs have effects of equal sign, interval mapping would give a QTL likelihood that is usually rather flat over a large chromosome region with a peak possibly somewhere between the two QTLs[12]. In MQM mapping, the QTL likelihood almost always shows clear peaks near the correct locations[12]. Only for composite interval mapping is the test at an intermediate interval always unaffected by the presence of the two QTLs. The problem of separating linked QTLs is illustrated in the first application (see later).

The power of QTL detection can be improved further when multiple traits are scored for the same plants[20] or when a single trait is scored on plants in multiple environments[20,21]. In the latter case, for instance, QTL likelihood maps are produced for each environment separately by interval mapping (see in the first application). But a joint analysis of all data – with terms for possible interactions between the QTL and environments – will offer improved power for QTL detection.

The results for power also hold for the precision of QTL localization, that is, precision may also be increased. The general rule is that precision is rather poor (i.e. the QTL is placed within an interval of 10 cM or more), if the chance of QTL detection is significantly less than 1.00 (Ref. 16).

Detection of markers near QTLs

The detection of markers near QTLs is the primary goal of QTL mapping. These markers will be used in marker-assisted breeding[24] or map-based cloning of genes[25].

In a statistical sense, a set of markers can be used to replace nearby QTLs in multilocus modelling. Various methods are available for statistical selection of these 'important' markers; other markers do not add extra information when fitting a multilocus model and are therefore 'redundant'[12,25]. One could start with no markers and add new important markers sequentially, or one could start with all markers of all chromosomes and drop redundant markers sequentially (if a dense map is available, one could also start with a subset of markers giving uniform coverage on all chromosomes). The forward selection imposes problems on the identification and separation of linked QTLs, as in interval mapping. Furthermore, backward selection is probably more powerful, since the unexplained variance is immediately reduced as much as possible, as in composite interval mapping and MQM mapping. Computational problems that occur when part of the marker data is missing, which is nearly always the case, have been solved[11,26]. Whether a marker is removed from or added to the multilocus model is based on the statistical test for its effect on the trait.

In MQM mapping it is recommended that a 2–16% significance level per marker test is used during the selection procedure. Markers in the final set can be tested at a genome-related significance level, or they can be used as genetic background control in the precision mapping of QTLs.

In the original composite-interval mapping approach no selection of markers is used – all markers outside the region of interest are used and the test for QTL activity in a given region is not affected by QTLs outside the region. This is the only way to solve the problem with many linked QTLs[13,14]. The cost of avoiding errors in QTL detection is loss of power, which is sometimes tremendous[12]. In MQM mapping, selection at a 2–16% significance level per marker test, however, removes clearly redundant markers. It has been shown that this can result in much higher power, whereas in many instances linked QTLs can still be separated well[12]. A similar approach is also possible in composite interval mapping[14]. It should be noted that the two methods are still

evolving and tend to become similar, at least for inbred-line crosses with fairly complete marker information.

Applications

Currently, interval mapping is widely used and many applications have been reported[2]. So far, only a few applications have been reported in which the new multiple-QTL methods (MQM mapping and composite interval mapping) have been applied to plants. Here, two such applications are presented, one concerning fundamental plant biology, the other concerning crop improvement.

Genetic and environmental control of flowering time in Arabidopsis

The flowering time of many plant species is regulated closely by environmental conditions, such as day length and temperature, ensuring reproduction under optimal conditions[27]. The genetics of flowering time has been studied extensively for the model plant *Arabidopsis*, often by screening for mutations in the progeny of crosses between different varieties[27]. It is probable that not all of the genes involved have yet been detected by mutation analysis (only genes have been found for which alleles exist that have a large trait effect). Recently, genetic mapping has been carried out to identify the genes involved[21]. At least 12 regions on the genome displayed QTL activity, and four of them showed significant interaction with environmental conditions. Also some QTLs were close to loci for which mutants are known, and the mutant loci are therefore good candidates for the QTLs. Interval mapping and MQM mapping were applied to the data; results for chromosome 2 are shown to illustrate the problems in separating linked QTLs with effects of equal sign (Fig. 2). Here, the situation is even more complex because of QTL–environment interaction. The increased precision of MQM mapping is because of the elimination of genetic variation induced by linked and unlinked QTLs and also the joint analysis of the data from the six environments.

Breeding for resistance to Fusarium *in lily*

Techniques using molecular markers provide breeders with powerful tools for the efficient characterization and use of QTLs in crop improvement programmes. In particular, breeding for the increased resistance of crops to diseases and pests forms one of the major challenges to breeders, aiming at a considerable reduction in the use of chemicals during crop production. *Fusarium* causes major problems in many crops[28]. Recently, a first and successful attempt has been made to identify QTLs for partial resistance to *Fusarium* in lily (*Liliaceae*)[19]. Three chromosome-segments displayed significant QTL activity and explained the major part of trait variation[19]. Traditional individual analysis of markers and MQM mapping were applied to the data. Results for one chromosome segment are shown to illustrate the improvement in power that can be attained by MQM mapping in a complex situation with very incomplete marker information (Fig. 3). The increased power is because of the recovering of information about the marker genotypes and also the elimination of genetic variation induced by unlinked QTLs.

Conclusions and future prospects

Recent analytical advances have significantly improved the power and precision of QTL mapping for complex plant traits. Progress has been made from single-QTL towards multiple-QTL methods and from separate to joint analysis of data concerning multiple traits or multiple environments. Also, progress has been made from methods for inbred species to methods for outbred species. However, it is expected that future developments will contribute to further improvements. The use of new analytical techniques[19,29] and high performance computing opens up ways for tackling complicated QTL mapping problems, for instance when data arise from multiple related crosses[30,31] or pedigrees. It seems likely that in many instances QTLs can be identified and characterized as precisely as many qualitative genes – the analytical discrepancy between qualitative traits (often only affected by a single major gene) and quantitative traits (often affected by many genes of which some may have major effects) is disappearing. Furthermore, the distinction between plant, animal and human genetic mapping is vanishing with the advent and use of these new analytic tools for complex genetic situations: outbred crosses between divergent lines can be used in lily and pig[32], recombinant inbred lines are available for *Arabidopsis* and mouse[33] and pedigree data have been collected for soybean[34] and humans[35] – in all cases, data could be analysed in similar ways.

References

1 Michelmore, R.W. and Shaw, D.V. (1988) Quantitative genetics: character dissection, *Nature* 335, 672–673
2 Tanksley, S.D. (1993) Mapping polygenes, *Annu. Rev. Genet.* 27, 205–233
3 O'Brien, S.J., ed. (1993) *Genetic Maps*, Cold Spring Harbor Laboratory Press
4 Sax, K. (1923) Association of size differences with seed-coat pattern and pigmentation in *Phaseolus vulgaris*, *Genetics* 8, 552–560
5 Lander, E.S. and Botstein, D. (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps, *Genetics* 121, 185–199
6 Lincoln, S.E. and Lander, E.S. (1989) *Mapping Genes Controlling Quantitative Traits with MAPMAKER/QTL* (Whitehead Institute for Biomedical Research Technical Report)
7 Jansen, R.C. (1992) A general mixture model for mapping quantitative trait loci by using molecular markers, *Theor. Appl. Genet.* 85, 252–260
8 Knapp, S.J. (1991) Using molecular markers to map multiple quantitative trait loci: models for backcross, recombinant inbred and doubled haploid progeny, *Theor. Appl. Genet.* 81, 333–338
9 Haley, C.S. and Knott, S.A. (1992) A simple regression method for mapping quantitative trait loci in line crosses using flanking markers, *Heredity* 69, 315–324
10 Martinez, O. and Curnow, R.N. (1992) Estimating the locations and the sizes of the effects of quantitative trait loci using flanking markers, *Theor. Appl. Genet.* 85, 480–488
11 Jansen, R.C. and Stam, P. (1994) High resolution of quantitative traits into multiple loci via interval mapping, *Genetics* 136, 1447–1455
12 Jansen, R.C. (1994) Controlling the type I and type II errors in mapping quantitative trait loci, *Genetics* 138, 871–881
13 Zeng, Z-B. (1993) Theoretical basis of separation of multiple linked gene effects in mapping quantitative trait loci, *Proc. Natl Acad. Sci. USA* 90, 10972–10976
14 Zeng, Z-B. (1994) Precision mapping of quantitative trait loci, *Genetics* 136, 1457–1468
15 Van Ooijen, J.W. (1992) Accuracy of mapping quantitative trait loci in autogamous species, *Theor. Appl. Genet.* 84, 803–811
16 Darvasi, A. *et al.* (1993) Detecting marker-QTL linkage and estimating QTL gene effect and map location using a saturated genetic map, *Genetics* 134, 943–951
17 Rebaï, A., Goffinet, B. and Mangin, B. (1994) Approximate thresholds of interval mapping tests for QTL detection, *Genetics* 138, 235–240

18 Churchill, G.A. and Doerge, R.W. (1994) Empirical threshold values for quantitative trait mapping, *Genetics* 138, 963–971
19 Jansen, R.C. (1996) A general Monte Carlo method for mapping multiple quantitative trait loci, *Genetics* 142, 305–311
20 Jiang, C.J. and Zeng, Z-B. (1995) Multiple trait analysis of genetic mapping for quantitative trait loci, *Genetics* 140, 1111–1127
21 Jansen, R.C. *et al.* (1995) Genotype by environment interaction in genetic mapping of multiple quantitative trait loci, *Theor. Appl. Genet.* 91, 33–37
22 Hackett, C.A. and Weller, J.I. Genetic mapping of quantitative trait loci for traits with ordinal distributions, *Biometrics* (in press)
23 Tanksley, S.D., Ganal, M.W. and Martin, G.B. (1995) Chromosome landing: a paradigm for map-based gene cloning in plants with large genomes, *Trends Genet.* 11, 63–68
24 Gimelfarb, A. and Lande, R. (1995) Marker-assisted selection and marker–QTL associations in hybrid populations, *Theor. Appl. Genet.* 91, 522–528
25 Hackett, C.A. (1995) Selection of markers linked to quantitative trait loci by regression techniques, in *Biometrics in Plant Breeding. Applications of Molecular Markers* (Van Ooijen, J.W. and Jansen, J., eds), pp. 99–106, CPRO-DLO
26 Rodolphe, F. and Lefort, M. (1993) A multi-marker model for detecting chromosomal segments displaying QTL activity, *Genetics* 134, 1277–1288
27 Coupland, G. (1995) Genetic and environmental control of flowering time in *Arabidopsis*, *Trends Genet.* 11, 393–397
28 Nelson, P.E., Toussoun, T.A. and Cook, R.J., eds (1981) Fusarium: *Diseases, Biology, and Taxonomy*, Pennsylvania State University Press
29 Xu, S. and Atchley, W.A. (1995) A random model approach to interval mapping of quantitative trait loci, *Genetics* 141, 1189–1197
30 Rebaï, A. and Goffinet, B. (1993) Power of tests for QTL detection using replicated progenies derived from a diallel cross, *Theor. Appl. Genet.* 86, 1014–1022
31 Rebaï, A. *et al.* (1995) Detecting QTLs with diallel schemes, in *Biometrics in Plant Breeding. Applications of Molecular Markers* (Van Ooijen, J.W. and Jansen, J., eds), pp. 170–177, CPRO-DLO
32 Andersson, L. *et al.* (1994) Genetic mapping of quantitative trait loci for growth and fatness in pigs, *Science* 263, 1771–1774
33 Crabbe, J.C., Belknap, J.K. and Buck, K.J. (1994) Genetic animal models of alcohol and drug abuse, *Science* 264, 1715–1723
34 Lorenzen, L.L. *et al.* (1995) Soybean pedigree analysis using map-based molecular markers: I. Tracking RFLP markers in cultivars, *Crop Sci.* 35, 1326–1336
35 Guo, S.W. and Thompson, E.A. (1992) A Monte Carlo method for combined segregation and linkage analysis, *Am. J. Hum. Genet.* 51, 1111–1126

Ritsert Jansen is at the Dept of Population Biology, Centre for Plant Breeding and Reproduction Research (CPRO-DLO), PO Box 16, 6700 AA Wageningen, The Netherlands.

Current trends

– articles of interest to plant scientists in recent issues of other *Trends* magazines

Mapping and manipulating quantitative traits in maize,
C.W. Stuber, **Trends in Genetics** 11, 477–481

QTL mapping in rice,
S.R. McCouch and *R.W. Doerge*, **Trends in Genetics** 11, 482–487

Cyclic AMP, the reluctant messenger in plants,
G.P. Bolwell, **Trends in Biochemical Sciences** 20, 492–495

The G-box: a ubiquitous regulatory DNA element in plants bound by the GBF family of bZIP proteins,
A.E. Menkens, U. Schindler and *A.R. Cashmore*, **Trends in Biochemical Sciences** 20, 506–510

γ-Tubulin and microtubule organization in plants,
H.C. Joshi and *B.A. Palevitz*, **Trends in Cell Biology** 6, 41–44

Plant–parasite interactions: has the gene-for-gene model become outdated?
R.W. Innes, **Trends in Microbiology** 3, 483–485

Sacrifice in the face of foes: pathogen-induced programmed cell death in plants,
R. Mittler and *E. Lam*, **Trends in Microbiology** 4, 10–15

Unravelling senescence: New opportunities for delaying the inevitable in harvested fruit and vegetables,
G.A. King and *E.M. O'Donoghue*, **Trends in Food Science and Technology** 6, 385–389

Chlorophyll degradation in processed foods and senescent plant tissues,
J.W. Heaton and *A.G. Marangoni*, **Trends in Food Science and Technology** 7, 8–15

Palaeo-ecophysiological perspectives on plant responses to global change,
D.J. Beerling and *F.I. Woodward*, **Trends in Ecology and Evolution** 11, 20–23